

The influence of cover on nesting Red-capped Plovers: a trade-off between thermoregulation and predation risk?

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Abstract

Some ground-nesting birds adopt a mixed strategy of nesting in the open, or under cover (e.g. vegetation). This may represent a trade-off between thermally favourable nest sites (covered) and those that enable the early detection and avoidance of predators (open). This study examined whether such a trade-off exists for Red-capped Plover *Charadrius ruficapillus*, whose eggs are preyed upon principally by Little Raven *Corvus mellori*. For real and artificial nests, nest temperatures under cover (real, $25.9 \pm 0.1^\circ\text{C}$; false, $16.2 \pm 0.5^\circ\text{C}$) were cooler than those in the open (real, $26.8 \pm 0.1^\circ\text{C}$; false, $17.4 \pm 0.9^\circ\text{C}$). Covered nests had more visual obstructions than open nests (covered, $65.5\% \pm 11.4\%$; open, $7.4\% \pm 2.8\%$) and a standardised measure of incubator escape distance, initiated by experimental human approaches, indicated incubators fled open nests at longer distances than for covered nests. Nests under cover showed a slightly (non-significant) higher probability of surviving one day (Daily Survival Rate [DSR] = 0.978) than those in the open (DSR = 0.950). For false nests containing model eggs, covered nests exhibited better survival to 10 days compared with open nests (20.4% vs. 4.7%). Thus, covered nests are associated with enhanced thermal environments and egg survival, but predators can approach the incubator more closely. Overall, the proposed trade-off between thermal and predation risks associated with nest sites appears to exist and explains the ongoing occurrence of nests in open and covered locations. (*The Victorian Naturalist* 131 (4) 2014, 115–127)

Keywords: shorebird, wader, microhabitat, *Charadrius ruficapillus*

Introduction

Depredation is among the most important factors influencing the rate of clutch loss for many avian species and accounts for up to at least 80% of all clutch failures across a variety of species, habitats and geographic locations (Ricklefs 1969; Martin 1993). High rates of clutch loss may result from the occurrence of superabundant generalist egg predators that opportunistically prey upon nesting birds and their eggs (Marzluff and Neatherlin 2006). Corvids are a common avian nest predator and are the most prominent egg predator of many ground-nesting birds (Angelstam 1986; Dwernychuk and Boag 1972; Yahner and Wright 1985). These generalist omnivores are highly adaptable and are increasing in numbers, taking advantage of the anthropogenic resources available to them in a highly urbanised world (Angelstam 1986; Marzluff 2001; Marzluff and Neatherlin 2006; Wallander *et al.* 2006).

Nesting birds employ a range of anti-predator strategies including crypsis (hiding the nest

and its contents) and active defence, including aggression and distraction (Byrkjedal 1989; Geering *et al.* 2007). Nest site selection (the choice regarding where a bird places its eggs) is one of the most important reproductive decisions (Thyen and Exo 2005; Smith *et al.* 2007) because it has a major influence on nest outcome (Angelstam 1986; Martin 1993; Gotmark *et al.* 1995; Santisteban *et al.* 2002; Tieleman *et al.* 2008). Once birds decide on a nest site and eggs are laid, the eggs cannot be moved and must survive the incubation period *in situ* if young are to hatch. Nest location also influences the prevailing thermal conditions for incubation, particularly for ground-nesting species whose nests do not feature structures which aid thermal insulation (Amat and Masero 2004a; Tieleman *et al.* 2008).

Cover and temperature

Incubation, the use of parental body heat to thermoregulate eggs (Blanken and Nol 1998)

is essential for the growth and development of avian embryos (Purdue 1976; Clutton-Brock 1991; Tieleman *et al.* 2008). Adults both warm and cool eggs as required (Grant 1982; Weston and Elgar 2007). For adult shorebirds that typically nest on the ground, thermoregulatory behaviours such as egg shading, heat transfer via the brood patch or belly soaking (Purdue 1976; Downs and Ward 1997; Geering *et al.* 2007) are employed to cool or warm the eggs to maintain optimal egg temperatures. In most avian species, optimal egg temperature for embryo growth and development ranges between 32°C and 35°C and lower and upper lethal temperature limits range from 25°C to 27°C and 43°C to 44°C, respectively (Tieleman *et al.* 2008). Many shorebirds nest on the ground with little or no insulation in nests (Amat and Masero 2004a). In areas with little or no cover, incubating birds and their eggs can be exposed to air temperatures in excess of 40°C and ground temperatures in excess of 50°C (this study). As egg temperature is positively correlated with ambient temperature (Purdue 1976; Weston and Elgar 2005), in areas where air temperatures can reach extremes, nesting adults and their developing embryos can be exposed to conditions that threaten egg viability through overheating (Alrashidi *et al.* 2010). Nesting under vegetation provides protection from the thermal extremes of wind and solar radiation (Amat and Masero 2004a; Kim and Monaghan 2005). Vegetation surrounding a nest acts as an insulator by blocking wind, and shade created by overhanging vegetation helps to create a more stable and thermally favourable microclimate (Amat and Masero 2004b; Kim and Monaghan 2005; Smith *et al.* 2007; D'alba *et al.* 2009).

Cover, crypsis and predator defence

In addition to providing thermal protection, cover may also provide protection from predators (Tieleman *et al.* 2008). Vegetative cover can be defined as any form of vegetation that provides crypsis, concealing or protecting an animal. There is great variation in the costs and benefits of nesting under cover or in the open (Table 1). With the risk of clutch depredation high in many avian species, the ability to detect the approach and proximity

of potential predators during nesting is likely to enhance defence of clutches, especially for passively defending species, which optimise nest crypsis by distancing themselves from the nest location in the proximity of predators. Nesting in the open also allows an incubating adult to better detect an approaching predator and maximise its own survival. An exposed open nest, however, also allows predators to better detect incubating adults and their nests from a distance. Cover may obscure the vision of an incubating parent from the nest, thus hindering its ability to detect approaching predators (Gotmark *et al.* 1995; Javurkova *et al.* 2011). This can prove particularly costly when the species requires early detection for escape (Smith *et al.* 2007) because cover can impede a bird's ability to escape the nest undetected (Wiebe and Martin 1998) and increase the risk of adult depredation (Wiebe and Martin 1998; Amat and Masero 2004a; Low *et al.* 2010).

Many birds that nest in open habitats (e.g. waders) have several adaptations to avoid detection by predators. Among these, some species move to environments where they can avoid terrestrial predators: Banded Stilts *Cladorhynchus leucocephalus*, for example, breed on isolated islands in ephemeral inland lakes (Geering *et al.* 2007). Incubating adult waders often exhibit cryptically coloured dorsal plumage presumably as camouflage, decreasing the likelihood of nest detection and clutch depredation (Wallander *et al.* 2006). Species may also lay cryptically coloured eggs (especially effective when the nest is left unattended) and some hide their nest under vegetation as a form of defence (Wallander *et al.* 2006). Parents employ distraction, aggression or crypsis in defence of their clutches (Geering *et al.* 2007; Ekanayake and Weston 2011).

Study aims

Species that can nest in either the open or under cover, may effectively trade-off between thermally favourable nest sites, and their view from the nest (i.e. overall safety from predators), when selecting nest sites (Gotmark *et al.* 1995; Wiebe and Martin 1998; Thyen and Exo 2005; Tieleman *et al.* 2008). This study investigated the benefits and costs associated with nesting under cover or in the open in the ground-nest-

Table 1. A partial review of studies investigating the influence of nest cover on the nesting success of bird species. NA means not applicable.

Authors	Species	Nest type	Climate	Most successful real nest cover type	Most successful false nest cover type
Amat and Masero (2004a)	Kentish Plover <i>Charadrius alexandrinus</i>	Ground	Hot	No effect of nest cover	NA
Tieleman et al. (2008)	Hoopoe Lark <i>Alaemon alaudipes</i>	Ground	Hot	No effect of nest cover	No effect of nest cover
Gotmark et al. (1995)	Song Thrush <i>Turdus philomelos</i>	Tree (low cup nests)	Temperate	No effect of nest cover	Covered nests
Dvornychuk and Boag (1972)	Ducks (six species)	Ground	Unknown	No effect of nest cover	Covered nests
Wiebe and Martin (1998)	White-tailed Ptarmigan <i>Lagopus leucurus</i>	Ground	Alpine	Covered nests	NA
Ludwig et al. (2010)	Black Grouse <i>Tetrao tetrix</i>	Ground	Cold	Covered nests	NA
Colwell (1992)	Wilson's Phalarope <i>Phalaropus tricolor</i>	Ground	Unknown	No effect of nest cover	NA
D'Alba et al. (2009)	Common Eider <i>Somateria mollissima</i>	Ground	Cold	Covered nests	NA
Kim and Monaghan (2005)	Herring Gull <i>Larus argentatus</i> and Lesser Black-backed Gulls <i>L. fuscus</i>	Ground	Temperate	Covered nests	NA
Schieck and Hannon (1993)	Willow Ptarmigan <i>Lagopus lagopus</i>	Ground	Cold	No effect of nest cover	NA

ing Red-capped Plover *Charadrius ruficapillus*, using real eggs and nests and model eggs in artificial (henceforth 'false') nests. Specifically, this study aimed to determine whether:

1. covered nests present incubating adults with a more favourable microclimate for nesting by maintaining more favourable (i.e. less extreme) nest temperatures; and
2. cover restricts the view from the nest of an incubating adult, affecting its ability to detect and react to potential approaching predators. These metrics represent indices of predation risk to adults, and also to eggs because the defence of eggs relies on the incubator's departure from the cryptic eggs before a predator approaches too closely.

Methods

This study was conducted at two neighbouring coastal wetland sites, in an urbanising landscape, in southern central Victoria, Australia: Cheetham Wetlands (37°53'56"S, 144°47'33"E; 420 ha) and Truganina Swamp (37°52'07"S, 144°48'12"E; 148 ha) (Antos *et al.* 2007). The area experiences a Mediterranean climate, with temperatures during the study period reaching a minimum of -1.7°C and a maximum of 47.5°C (Bureau of Meteorology 2012). Due to the close proximity of the two sites and the fact that Red-capped Plovers and their primary predator (Little Raven *Corvus mellori*) move between these sites (unpubl. data), data is pooled across sites. The study areas are substantial and apparently suitable nest sites abound (both covered and in the open).

Nest monitoring

Nests were located between July 2011 and February 2012 by searching regularly in and around ponds containing suitable nesting habitat (for seasonal variation in the occurrence of nests under cover and in the open, we draw upon data that was collected starting in 2010, and for response distances we draw upon nests recorded from mid-2011 to mid-2014). Red-capped Plovers almost always nest in new locations (within or between pairs), and there is no 'traditional' use of specific nests. Once a nest was located, the expected hatch date was estimated to enable success rates of nests to be estimated. Eggs were aged using the flotation

method (Liebezeit *et al.* 2007) and estimated hatch date was calculated assuming a 30-day incubation period. Nests were then visited around this estimated date to determine hatching success. Incubating adults were caught by using walk-in nest traps (see for example, Cardilini *et al.* 2013). Captured individuals were banded with a metal band placed on the tarsus and an orange flag engraved with a unique two-letter combination on the tibia. This combination was used later to identify individual adults and often aided in establishing whether some nests were successful or had failed by observing a brood accompanying the flagged adult/s (see Lees *et al.* 2013).

Following hatching or failure, nest site characteristics were recorded. Nest cover (any vegetation dead or alive directly above the nest) was indexed for each nest by placing a circular 10.5 cm diameter quadrat in the nest scrape, and counting the number of 12 x 12 mm grids visible (88 grids in total) from directly above. The percentage of visible grids was calculated and a cover type (open or covered) allocated. A covered nest was defined as having $\geq 10\%$ of the grids covered.

Thermal environment

Temperature loggers (Thermodata™ thermochron iButtons) were used to index nest temperature. They were placed in real nests just under the surface of the scrape and were programmed to record temperature once every hour for 10 days. Loggers were deployed only in nests ≥ 10 days old, ensuring laying had ceased. Ambient temperatures were recorded using iButtons suspended in shade 50 cm above the substrate. To test for an effect of incubation and cover on nest temperature, temperature loggers were also deployed in false nests (see below). For analysis of day and night temperatures, night was defined as the hours of 2100–0600 and day 0700–2000; this reflected periods of light and dark during the study period.

Indexing incubator detection and response to predators

Flight Initiation Distance (FID), the distance between predator and prey when escape begins (Weston *et al.* 2012) was used in this study as a reliable measure of predator detection by incu-

bators (see Guay *et al.* 2013a). To obtain FID, the investigator approached incubators from a distance that maximized the Starting Distance (SD) (e.g. Guay *et al.* 2013a, b, c). For open nests minimum SD was the distance at which the incubating adult was visible on the nest and could clearly see the investigator; for covered nests SD was defined as the distance at which the vegetation covering the nest could be seen by the investigator from the direction of approach. For FID, we supplemented our data for the 2011/12 season (collected by SL) with estimates collected during the 2013/14 breeding season (collected by LXT). A General Linear Model (GLM) revealed no difference between logSD between observers/seasons ($F_{1,42} = 0.534$, $P=0.135$) but a significant difference in logSD between covered and open nests ($F_{1,42}=9.314$, $P=0.004$). Longer SDs for open nests may obscure the effect of cover on FID (see McGriffin *et al.* 2013). Thus, we elected to adjust FID for SD, where FID_{adj} is the FID at the average SD (both logged), derived from a linear regression of logFID against logSD ($F_{1,45}=32.900$, $P < 0.001$, $R^2=0.428$). The adjustment: (1) used the slope of the relationship to obtain the model estimate of FID at average SD, and (2) then involved the addition or subtraction of the appropriate residual values. Nests were then approached directly at a constant walking pace until the bird fled the nest (i.e., FID). Distances were recorded using a laser rangefinder (after Glover *et al.* 2011).

Each nest for which an FID was recorded was assessed for visibility of the incubator from the nest (henceforth 'nest visibility') after the nest had hatched or failed. Visibility was measured by taking photographs (Lumix FT2, 14.1 Mega Pixel [MP] camera) from the nest scrape facing an 89 x 60 cm panel placed at each compass point (four in total to survey a bird's field of vision) and above the nest, each at a distance of 1 m from the nest. Each panel had 54 square 4 x 4 cm grids marked on it and photographs were examined to determine the number of grids obscured by cover.

Egg survivorship and predation risk

False nests with model eggs were deployed across the study site as a method of indexing depredation rates. Although depredation rates

of model eggs may not mimic that of real nests, they may be used to determine relative differences in depredation between habitats (Angelstam 1986; Willson *et al.* 2001). To determine any seasonal variation in depredation rates, the experiment was repeated five times (September to February excluding October), but all repeats involved new nest locations. The experiment was a simple single-factor design to determine depredation rates on open versus covered nests. The first experiment (September) incorporated a second factor, namely the use of remote sensor cameras (Scoutguard™: 5MP ultra Compact digital scouting/trail camera, DTC-530 V, HCO Outdoor Products) to monitor half of the false nests (stratified across the cover and open treatments) to identify egg predators. Due to the overwhelming depredation rate on camera-monitored nests, subsequent deployments did not involve the use of cameras.

The number of nests and eggs deployed, and in some cases the occurrence of nest checks, was influenced by unanticipated flood events. On average 74 false nests were deployed at least 100 m apart and at random locations throughout the study site (no site was reused) and were randomly allocated a cover treatment (open or covered). Each nest, a small depression in the substrate, contained two Japanese Quail *Coturnix japonica* eggs that were chosen because they best resemble those of Red-capped Plovers. Nests were monitored for a 30-day period to mimic plover incubation duration and checked at regular 10-day intervals after deployment to establish nest depredation rates and to retrieve any deployed temperature loggers.

Real nests were visited weekly to determine nest success or fate (here, 'success' describes the likelihood of hatching and 'fate' refers to the cause of failure; after Cardilini *et al.* 2013) and was classified as either depredated, flooded, abandoned or successful. Due to the imbalance between clutches depredated and those that were successful (87.5% failed), the application of many statistical approaches such as logistic regression was not possible. Alternatively, to determine any differences in clutch survival between open and covered nests, daily survival rate of nests (DSR, the probability that a nest would survive one day) was calculated using Mayfield's method (Mayfield 1961, 1975).

Statistical analysis

Standard statistical procedures were followed for all analyses as outlined in Quinn and Keough (2002). Mixed modeling, correlation analysis and general linear models (GLMs) were performed in Statistical Package for the Social Sciences (SPSS), version 18.0 (SPSS Inc. Chicago, Illinois), Daily Survival Rate (DSR) calculations and contingency table (χ^2) analysis were performed manually in Microsoft Excel, version 2010. To calculate exposure days required for DSR analysis, GLMs were used within the package MASS in the statistics software package R, version 2.11.1. (R Development Core Team). Summary statistics are presented as means \pm one standard error (unless otherwise stated). Graphs, temperature data and percentage data are all presented with raw untransformed data to enhance readability and do not imply normality of data.

Results

Eighty-nine nests were discovered of which 29 (33%) were under cover and 60 (67%) were in the open (Fig. 1). Of those, 72 clutches (81%) were depredated, nine (10%) were successful, five (6%) were abandoned and three (3%) were flooded. Sixteen chicks hatched from the nine successful nests; however, none survived to fledge. An examination of data from 2010 to 2012 ($n=191$ nests), revealed that covered and open nests were located throughout the breeding season (Fig. 2). For those months in which at least 10 nests were recorded, the percentages of covered nests were: 72.0%, September; 77.8%, October; 58.6%, November; 54.3%, December; 58.2%, January; and 75.0%, March.

Thermal monitoring

Residuals of the relationship between false nest temperature and ambient temperature were derived from a linear regression which was selected using the curve fit procedure on SPSS; $\log_{10}(\text{Ambient } ^\circ\text{C})=0.730 * \log_{10}(\text{False Nest } ^\circ\text{C}) + 0.348$ ($R^2=0.676$, $F_{1,12051}=25118.420$, $P < 0.001$). Thus, high residual values (absolute) indicate greater deviation from this model, positive values indicate hotter temperatures than modelled, and negative residual values indicate cooler temperatures than modelled. Residuals were used as the response variable

for subsequent mixed modelling of the influence of cover on false nest temperatures. The mixed model included a random factor of nest identity to control for repeated sampling of the same nest. This mixed model indicated that open false nests were warmer than those under cover (open nests compared with covered, coefficient=0.0182, $t=10.255$, $p \leq 0.001$; Fig. 3). In terms of actual temperature this represents a mean difference of 1.2°C (open, $17.4 \pm 0.9^\circ\text{C}$, $n=17$ nests; covered, $16.2 \pm 0.5^\circ\text{C}$, $n=26$ nests).

Some real nests being thermally monitored were preyed upon or hatched before collection of the loggers, necessitating truncation of the sequence of the thermal data, such that it represented only those periods during which eggs were being incubated. To truncate sequences, thermal data from nests were inspected for minimum temperatures recorded across a 24-hour period. Of the 17 nests surveyed, incubation had ceased prior to logger collection (temperature $\leq 18^\circ\text{C}$) in five nests and the thermal data preceding this date were excluded. Of these nests, one data set was excluded entirely due to incorrect temperature readings. Residuals of the relationship between real nest temperature and ambient temperature were derived from a linear regression which was selected using the curve fit procedure on SPSS; $\log_{10}(\text{Real } T \text{ } ^\circ\text{C})=0.474 * \log_{10}(\text{Ambient } T \text{ } ^\circ\text{C}) + 0.775$ ($R^2=0.546$, $F_{1,3936}=4733.363$, $P \leq 0.001$). Residuals were used as the response variable for subsequent mixed modeling of the influence of cover on real nest temperatures. The mixed model included a random factor of nest identity to control for repeated sampling of the same nest. This mixed model indicated that open real nests were warmer than those under cover (open nests compared with covered, coefficient=0.006, $t=3.504$, $p \leq 0.001$; Fig. 3). In terms of actual temperature this represents a mean difference of 0.9°C (open, $26.8 \pm 0.1^\circ\text{C}$, $n=9$ nests; covered, $25.9 \pm 0.1^\circ\text{C}$, $n=7$ nests). The presence of an incubating parent warmed the nest (Fig. 3), indicating that the nest temperatures indexed the temperatures experienced by the eggs. With nest temperatures around 9.4°C warmer in the open and 9.7°C warmer under cover than temperatures recorded in false nests, real nests were maintained at a higher temperature both during the day and night (day, 27.4

$\pm 0.1^\circ\text{C}$; night, $23.5 \pm 0.1^\circ\text{C}$, $n=16$ nests) than false nests (day, $18.4 \pm 0.1^\circ\text{C}$; night, $13.6 \pm 0.1^\circ\text{C}$, $n=43$ nests).

Depredation risk

A potential cost of nesting under cover is that the ability to detect incoming predators may be reduced by visual obstructions around the nest. The number of panel grids visually obstructed from the nest per panel was highly correlated between panels ($r_{\text{Pearson}} 0.504 - 0.946$; all P s ≤ 0.012 ; $n=24$) and therefore were summed to characterise overall visibility from the nest (henceforth the total number of panel grids visually obscured ($\text{Obs}_{\text{Total}}$). $\text{Obs}_{\text{Total}}$ was also highly correlated with the estimate of cover over a nest from the circular quadrat ($r_{\text{Pearson}}=0.888$, $P \leq 0.001$, $n=24$) so $\text{Obs}_{\text{Total}}$ was selected for analysis. $\text{Obs}_{\text{Total}}$ was substantially and significantly higher for covered nests (79.2 ± 3.0 % grids covered, $n=11$ nests) than open nests (5.2 ± 1.2 %, $n=13$ nests) ($t=17.95$, $df=22$, $p \leq 0.001$).

Forty-six nests were approached to examine whether covered nests were associated with higher FIDs than open nests. The low clutch survivorship of real nests limited the number of FIDs obtained and therefore the number of nests used in FID analysis. Covered nests had more visual obstructions compared with open nests (panels facing the direction of investigator approach [$\text{Obs}_{\text{Approach}}$], 2011/12 data only; covered, $65.5 \pm 11.4\%$, $n=11$; open, 7.4 ± 2.8 %, $n=13$; $t=5.367$, $df=15.418$, $p \leq 0.001$). The influence of cover on FID was investigated by running a GLM of FID_{adj} on the two-level factor of 'covered' or 'open'. FID_{adj} for incubators of covered nests was significantly shorter compared with those incubating in the open ($F_{1,44}=7.174$, $P=0.010$; Table 2). Importantly, SD was higher for open compared with covered nests (see Methods), indicating that open nests were associated with greater distances at which potential predators could be detected.

Egg survivorship and predator pressure

Of 38 nests on which cameras were deployed, cause of clutch loss could be determined in 86.8% (33) of cases. In every case where a predator was detected, Little Ravens were the predator. For the subset of false nests with cameras

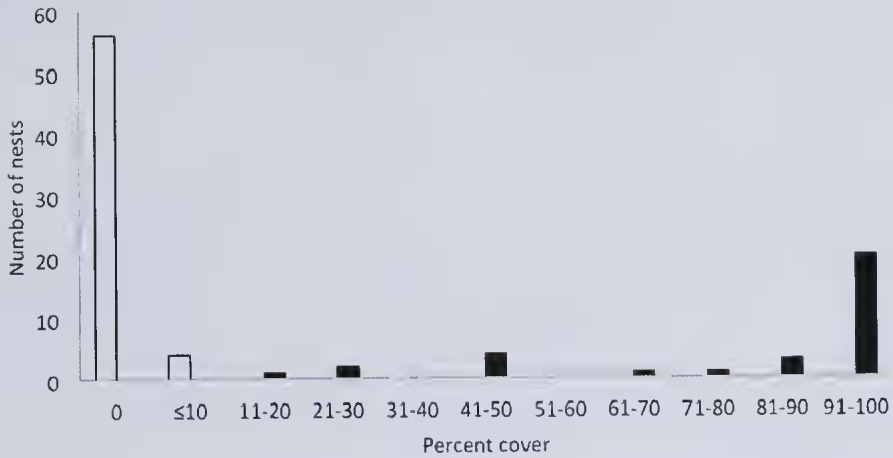


Fig. 1. The frequency distribution of nests found under varying degrees of cover as measured by the percentage of obscured grids of a circular quadrat placed in the nest scrape, when viewed from above. Open nests are shown as hollow bars and nests under cover are shown as solid bars.

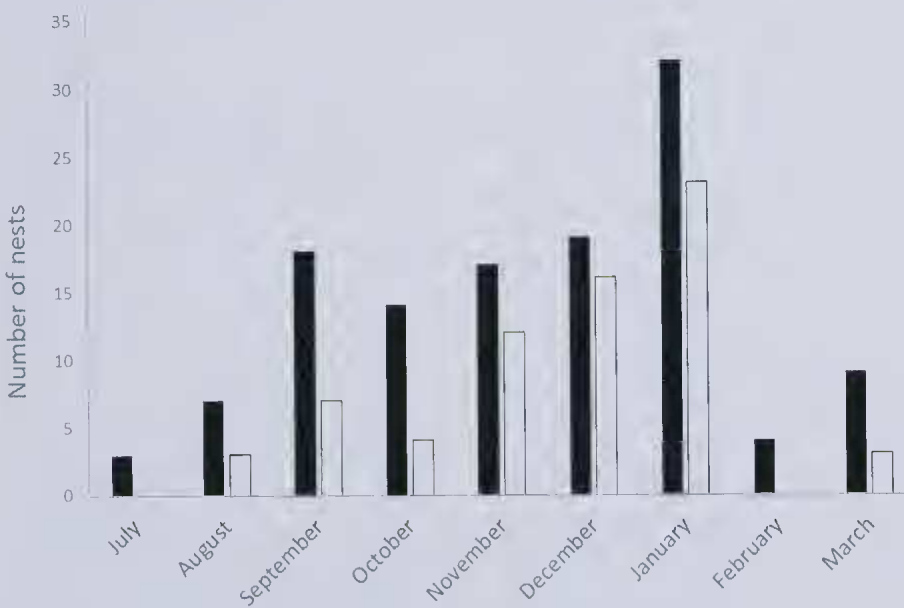


Fig. 2. The number of covered (solid bars) and open (hollow bars) nests in different months of the year, pooled across seasons, 2010 to 2012 (n = 191 nests).

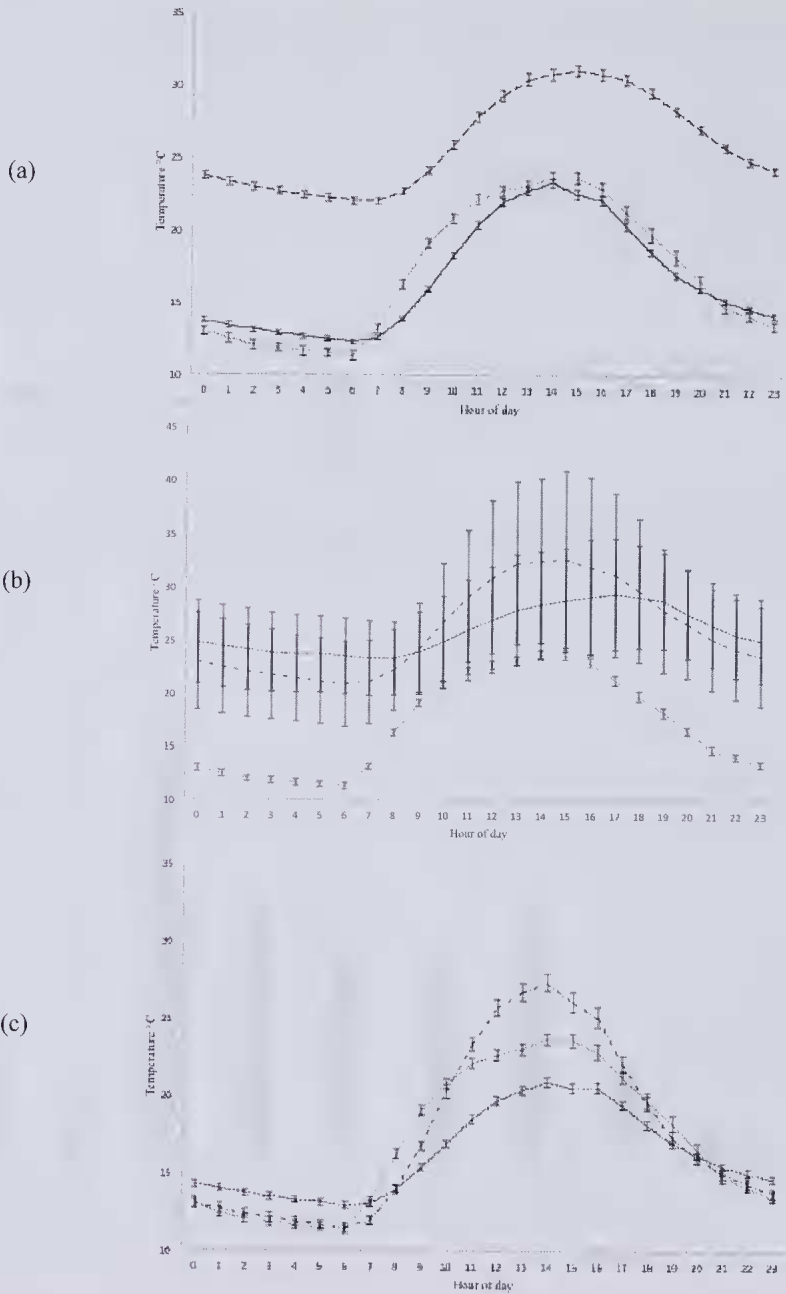


Fig. 3. Mean and standard error of temperature loggers in real and false nests, and at ambient temperature stations, recorded across a 24-hour period (midnight = 0). In each panel, ambient temperature is shown as a grey line. (a) Real nests (dashed line, $n = 16$) and false nests (solid line, $n = 43$); (b) real open nests (dashed-dot line, $n = 9$) and real covered nests (dashed line, $n = 7$); and, (c) false open nests (dashed-dot line, $n = 17$) and false covered nests (dashed line, $n = 26$).

Table 2. Mean and standard error of flight initiation distance (FID), starting distance (SD) and the log of FID adjusted to average SD ($\log FID_{adj}$), for covered and open nests (in metres).

Variable	Covered	Open
FID	37.636 ± 9.163	67.154 ± 11.718
SD	62.909 ± 13.810	95.077 ± 13.932
$\log FID_{adj}$	1.404 ± 0.192	1.869 ± 0.078

versus no cameras, overall take rates to the 10-day check were high (92.2%) which precluded statistical comparison of nests with and without cameras. Nests with cameras ($n=40$) did not survive beyond 10 days while six nests without cameras ($n=37$) survived. To remove any influence of cameras on already high take rates, the use of cameras was suspended for subsequent deployments (the time to depredation after camera deployment, in hours [logged], did not differ between covered and open nests; $t=0.070$, $df=30$, $P=0.945$).

Of 317 false nests (without cameras deployed), 12.9 % (41) of model clutches survived the first 10 days, 6.6 % (21) to 20 days and 4.7 % (15) to 30 days. The low survival of model clutches meant survival to 10 days was selected for further analysis. Moreover, the imbalance between model clutches preyed upon and those that survived precluded the meaningful application of a number of analytical approaches such as logistic regression. Survival of false nests with model clutches was low, reaching a trough in December before survival improved in January and February 2012 (Fig. 4). For false nests without cameras, covered nests (20.4%) exhibited better survival to 10 days compared with open nests (4.7%) (contingency table, $\chi^2=17.281$, $df=1$, $P \leq 0.001$).

Of the 89 nests found across the study period, 82 were appropriate to use in analysis of daily survival rate (DSR). Mayfield's estimate of DSR revealed that nest cover did not influence the survival of real nests ($t=0.030$, $df=80$, $p \leq 0.976$). Although non-significant, nests under cover showed a slightly higher probability of surviving one day (DSR, 0.978 ± 0.009 ; 95% CI, 0.995 - 0.961) than those in the open (DSR, 0.950 ± 0.007 ; 95 % CI, 0.963 - 0.936).

Discussion

Findings from this study supported the predictions that (1) covered nests experienced a

cooler and more stable thermal environment for incubation than nests in the open, and that (2) enhanced predator detection and response (as indexed by human approaches) was associated with open nests.

Thermal environment

In an environment where nesting sites are not limiting and ground temperatures can be in excess of 50°C (this study), this study has demonstrated that incubating Red-capped Plovers gain a thermal advantage during incubation by nesting under vegetative cover, with cover protecting nests and their contents from the thermal extremes, presumably by buffering from wind and sun. This results in cooler nest temperatures being maintained in covered nests, while those in the open experience higher nest temperatures (the magnitude of the difference in temperatures should not be regarded as absolute; we indexed these temperatures). Studies of other ground-nesting birds have demonstrated a similar thermal advantage when nesting across a range of climatic zones and species (Amat and Masero 2004b; Kim and Monaghan 2005; D'alba *et al.* 2009). Methods of sampling nest temperature are diverse; for many studies temperature probes are deployed in eggs (Amat and Masero 2004b), away from the nest scrape (Kim and Monaghan 2005) or in the nest scrape itself (D'alba *et al.* 2009) to obtain thermal data. The diversity of sampling methods and the fact that similar results were obtained across all studies further highlights the influence of nest cover on nest temperature and validates our method of indexing temperature. The difference in nest temperature between open and covered nests suggest that Red-capped Plovers in the open may need to engage more egg and adult thermoregulatory behaviours when nesting compared to those that nest under cover. Amat and Masero (2004b) showed that female Kentish Plovers *C. alexandrinus* that nest in the

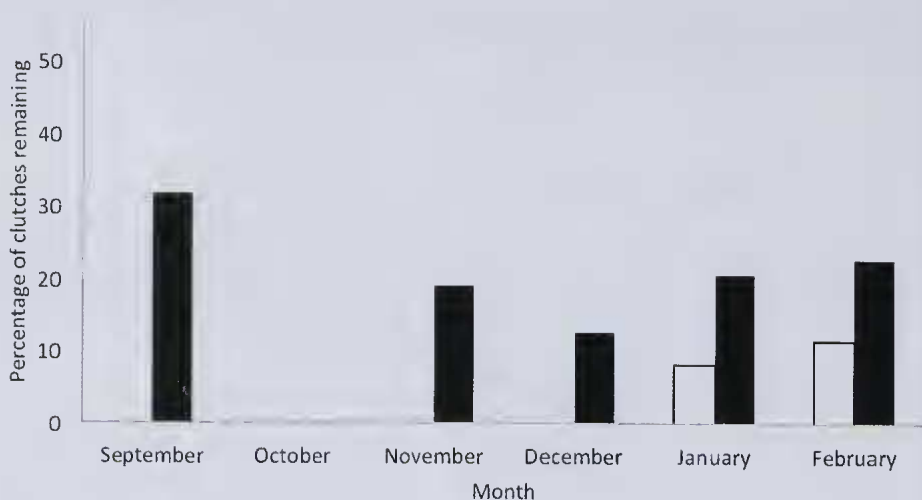


Fig. 4. Percentage of false clutches remaining after the first 10-day check ($n = 317$ nests) for each calendar month between September 2011 and February 2012. Open nests are represented by open bars and covered nests by solid bars. False nests were not deployed during October.

open and experience warmer temperatures, display behaviours indicative of heat stress such as panting, gaping and belly-soaking, while those that nest under cover in a cooler environment do not. The possibility of these behaviours being adopted by Red-capped Plovers is unknown; however, this would be worthy of further study. Additionally, the need for greater thermoregulation may compromise the crypsis of open nests (e.g. through more frequent change-overs of incubators), and this warrants further study.

This study revealed that covered and open nests were used throughout the breeding season. Under the hypothesis that nest selection is flexible within birds (most of the study birds re-nest within a season; unpubl. data), it might be tempting to predict a seasonal shift to cover during hotter months (or a similar shift in regard to any seasonal fluctuations in predator occurrence or activity). However, we caution against interpreting these data in this way, without correcting for relative detectability and survival, variation in the availability of covered and open areas, differences between seasons, and interactions between seasonal variation in climate and predators. Such a study would be

a useful further endeavour but is beyond the scope of the present study.

Predators

Vegetative cover surrounding a nest obscures the view of an incubating adult of its surrounding environment, and could potentially lead to a reduced ability to detect the approach or proximity of potential predators (Gotmark *et al.* 1995; Javurkova *et al.* 2011). We showed that nest cover obscures the vision of the surrounding environment for incubators of covered nests to a greater degree than for incubators of nests in the open. We also showed that the distance at which detection of an approaching 'predator' (a human) occurs is considerably longer for open nests.

FID was shorter for Kentish Plover nests with more visual obstructions (covered) (Amat and Masero 2004a). This trend also occurs for many species of reptiles and amphibians that display longer FIDs in the open than under cover (Cooper 2006; Martin and Lopez 2000; Martin *et al.* 2006). Similarly, we report that cover is associated with shorter response distances for incubating Red-capped Plovers. Theoretically, the effect of cover on response distance could be reduced if incubators respond to alarm sig-

nals of their 'off-duty' partner (Beletsky 1989; Colombelli-Negrel *et al.* 2011; Leavesley and Magrath 2005). However, in our study this did not apparently occur.

Starting distance (SD) is commonly found to influence the response distance (FID) of birds to approaching predators (e.g. Blumstein 2003; McLeod *et al.* 2013; Symonds *et al.* 2014). Thus, the longer an incubating bird has to detect and assess an approaching risk or predator (i.e. a longer SD), the earlier it flees its nest. This study found higher SDs for open nests, again suggesting that potential predators are detected at longer distances at open nests.

Many generalist predators such as corvids are well adapted to urban areas because they use many anthropogenic resources available to them. Point Cook is a highly urbanised area and is predicted to grow in size in the future (Antos *et al.* 2007) possibly creating an ideal environment to support large corvid populations. Predator indexing in this study revealed that Little Ravens were the main predator acting on Red-capped Plover nest success, preying upon 100% of monitored false clutches. This result was not surprising because the surrounding area provides an ideal habitat to support large raven numbers and past studies on the nesting success of plovers in this area attributed clutch loss primarily to this predator (Cardilini *et al.* 2012); Whisson *et al.* unpubl. data).

Despite a slightly higher survival rate for covered nests, this study revealed no real advantage to clutch survival through nesting under cover or in the open, as daily survival rate (DSR) did not differ significantly between the two nesting habitats (though the false nest experiment revealed greater clutch survival under cover). Studies investigating an effect of nest cover on clutch survival vary in their conclusions with some showing no effect (Table 1). This is particularly true of real nests, suggesting the behaviour of an adult at the nest may have some effect on clutch depredation rate (Andersson and Wiklund 1978; Davison and Bollinger 2000). The real nests we studied apparently did not vary in survivorship between cover and open (see also Gotmark *et al.* 1995), though a greater sample size may have revealed a significant difference. Predators

search for prey using different techniques and they often rely on visual cues (e.g. avian predators) or an acute sense of smell (e.g. many mammalian predators). Vegetative cover can influence the effectiveness of these search techniques differently and can vary depending on the habitat and predator involved (Ludwig *et al.* 2010; Santisteban *et al.* 2002). Many studies, including the current study, report that false nests under cover exhibit higher survival than those in the open (Brand and George 2000; Dwernychuk and Boag 1972; Gotmark *et al.* 1995; Santisteban *et al.* 2002).

Is nest site selection a trade-off?

Studies investigating the thermal and predator environments of birds during nesting suggest that species with a choice of nesting in the open and under cover employ a trade-off between thermally favourable nest sites, view from the nest and safety from predators when choosing nest sites (Gotmark *et al.* 1995; Tieleman *et al.* 2008; Wiebe and Martin 1998). This study reports a clear thermal advantage to cover, but found no egg survival advantage to nesting under cover (for real nests). Predators can apparently get closer to incubators in covered nests. The fact that Red-capped Plovers nest in both habitats suggest there is a balance of benefits and costs to both options, and these may lie in hitherto unstudied aspects such as incubator stress or survival (LXT, unpubl. data).

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Bird's eggs in a coastal nest. Photo by Michael A Weston